

Natural recolonization of a productive tropical pond: day to day variations in the photosynthetic parameters

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ABSTRACT

Chlorophyll pigments (CHL), primary productivity (PP) and particulate nitrogen (N_p) in relation to several environmental factors were monitored during planktonic colonization of an aquaculture pond (Layo, Côte d'Ivoire). How interactions between the organisms are established in an initially azoic environment were investigated. From March, 15 (D1) to March, 31 (D16), the system transformation went through three stages. First, a precolonization by heterotrophic microbial community from D1 to D2 ($N_p < 1 \mu\text{m}$ maximum at D2: 243 mg m^{-2} ; CHL around 0). Then, a pioneer microalgal community developed from D3 to D7 (maximum CHL on D6: 19 mg m^{-2} ; PP: $1.0 \text{ g C m}^{-2} \text{ d}^{-1}$) with a significant contribution of picoplankton (CHL and PP $< 3 \mu\text{m}$: 33 and 23% of the total, respectively). Finally, a second microalgal colonization was noticed from D9 to D12 (maximum CHL: 55 mg m^{-2} , PP: $2.8 \text{ g C m}^{-2} \text{ d}^{-1}$), largely dominated by nanoplankton (CHL and PP $> 3 \mu\text{m}$: 95 and 99% of the total, respectively). Overall, photosynthetic activity appeared to be closely linked to algal biomass. The study of autotrophic biomass and activity in different size classes in relation to the other parameters allowed us to precise the origin of the biomass fluctuations. The first bloom appeared to be controlled by selective grazing on small algae. The second algal development ended when N requirement represented at least 69% of N supply (in the N-NH₄ form). This control was enhanced by the appearance of rotifers, leading to a more complex equilibrium.

The seasonal refilling of a pond, the first filling of a lake closed by a dam, or the installation near sea-surface of deep water under wind effects are as many possibilities of studying colonization phenomena in virgin water. This approach is especially interesting for describing ecological successions and analyzing their different levels of organization. During the first phase of a colonization process (first hours or days), the system is free of complex trophic cross-relations which appear in steady state conditions. The Layo aquaculture ponds, near Ebrié lagoon (Côte d'Ivoire), used for fish-breeding with artificial food (Hem et al. 1990) are suitable systems for the study of natural colonization processes. They are directly filled by

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ground water, and, indirectly, by Ebrié water through the lagoon banks (Guiral and Ferhi, submitted). Exchanges are only possible by the air-water interface (light, rain, evaporation) and the water-sediment interface (water, ionized compounds and nutrients). Their surface is about 600 m², with a volume ranging from 300 to 600 m³, depending on ground water level. Their limited depths (maximum 1 m) reduce hydrodynamic phenomena to thermal convections, and wind-induced circulation is limited by the surrounding banks. Density stratification owes mainly to thermal differences, and nutrients entering through sediment are distributed into the entire water column. The ponds are periodically drained off, cleaned out and lime is spread. After a few weeks of natural evolution (filling and planktonic colonization), fry are introduced.

The main processes of the biological colonization in a Layo pond were described by Legendre et al. (1987), but sampling was carried out during several weeks with 4 to 10 days time-interval. In order to describe more extensively the different early colonization stages and their succession, a two-week study was conducted in March 1988, with a more intensive sampling lag (1 to 2 observations per day). The present work on phytoplanktonic colonization is part of a program aiming at a better understanding of the dynamic organization of such a system. In this perspective, primary productivity and its control in different size classes of phytoplankton were determined throughout the colonization process.

Material and Methods

The pond, situated in the Layo aquaculture station near the Ebrié lagoon (5N, 5W) has a surface of about 600 m². The pond was completely drained off in the afternoon of March 14, 1988 and lime was spread (0.2 kg CaCO₃ m⁻²). The study was conducted between March 15 (D1) and 30 (D16). Water level raised from 0.15 m (D1) to 0.60 m (D16), increasing the volume from 86 to 352 m³. The natural refilling of the pond is due to different inputs of water, originating from ground water, Ebrié lagoon through the banks and local rainfall.

1. Sampling, physical and chemical characteristics

Discrete sampling for seston was conducted at 8 am (an additional sampling was done at 6 pm during the first 10 days, and data were averaged) at the center of the pond with a peristaltic pump. The pipe was acid-washed and rinsed with pond water before sampling. Water was filtered on a 63 µm screen at the pump outlet. Particulate matter > 63 µm was collected with a 10 l vessel and prefiltered onto 250 µm mesh size. Ammonia was measured every 2 hours (indophenol blue method, Grasshoff and Johannsen 1972), and averaged daily. Oxygen concentration was automatically recorded every 10 min (oxygen probe YSI 57 and stirrer suspended 0.10 m below the surface). The global incident irradiance (PYR) was measured with a LiCor 200SB pyranometer (units and abbreviations: Table 1). Photosynthetically Active Radiation (PAR, 400–700 nm) was estimated to around 50% of PYR (Jitt et al. 1976;

Table 1. Abbreviations and units used in the text

Abbreviation	Unit	Formula or expression
Z	m	Depth
PYR	Wh m ⁻²	Global incident irradiance
PAR ₍₀₎	mole _q m ⁻² d ⁻¹	Photosynthetically active radiations, subsurface level can be expressed in kJ m ⁻² d ⁻¹
ε	m ⁻¹	Light attenuation coefficient
CHL	mg m ⁻³	Chlorophyll a concentration, can also be expressed in mg m ⁻²
PROD	g C m ⁻² d ⁻¹	Primary production; can be expressed in kJ m ⁻² d ⁻¹ or mole C m ⁻² d ⁻¹
K _C	m ² (mg CHL) ⁻¹	Phytoplankton specific light attenuation (for this work: 0.0072)
P _B	mg C (mg CHL) ⁻¹ h ⁻¹	Assimilation number, PROD expressed in mg C m ⁻³ h ⁻¹ .
E	%	Global efficiency, PROD by PAR ₍₀₎ ratio, both expressed in kJ m ⁻² d ⁻¹
E _B	% (mg CHL) ⁻¹	Efficiency by biomass unit
Φ _Z	mole C mole _q ⁻¹	Quantic efficiency (quantum yield), P _{B(Z)} expressed in mole C (mg CHL) ⁻¹ h ⁻¹ Φ _Z = P _{B(Z)} * PAR _(Z) ⁻¹ * K _C ⁻¹

Morel 1978; Coté and Platt 1983). Air-water immersion effects reduce PAR by 25% (Morel 1978), and the energy available for microalgae is then close to 37.5% of PYR. A Li 193SB spherical quantum meter immersed every 2 h at different levels allowed an estimation of the light attenuation coefficient (ε). The ε of the day was taken from the average of the ε calculated from 8 am to 6 pm.

2. Particulate matter

Size fractionation in the whole study was conducted on Nuclepore membranes (1 and 3 µm pore size) and on nylon mesh (63 and 250 µm mesh size). Weights of organic and inorganic seston were obtained by weighting material recovered by filtration onto Whatman GF/F filters before and after 6 h combustion at 550 °C. Particulate N concentrations (N_p) were determined with a Leco CHN analyzer. Photosynthetic pigments reflecting the microalgal biomass in < 1, 1–3 and 3–63 µm size classes were determined with a Turner 111 fluorometer after methanol extraction (Yentsch and Menzel 1963). Size fractionations gave an estimate of respective contributions to the total algal biomass of picoplankton (1 to 3 µm) and larger cells, here assimilated to nanoplankton. Spectrophotometric controls indicated that chlorophyll a was the predominant chlorophyll pigment throughout the study. A linear regression between the chlorophyll concentrations and ε furnished an estimate of K_C, the specific light attenuation coefficient for chlorophyll a (Kirk 1983; Dubinsky et al. 1984).

3. Primary production, efficiency parameters

Primary production was estimated as autotrophic fixation of CO_2 . The assimilation of labelled CO_2 ($\text{Na}_2^{14}\text{CO}_3$; CEA, France) was conducted in light and dark 125-ml bottles, filled with subsurface (0.10 m) water and incubated 2 to 3 h at every 0.10 m (2 replicates for each level). Size fractionation after incubation was done under slight depression on 1 and 3 μm pore size Nuclepore membranes. Dissolved inorganic C concentrations were derived from total alkalinity (Gran 1952), conductivity, temperature and pH (Stumm and Morgan 1970). Primary production ($\text{mg C m}^{-3} \text{ h}^{-1}$) was integrated for space and time ($\text{mg C m}^{-2} \text{ d}^{-1}$) using the trapezoidal rule. The energy corresponding to 1 g of biologically fixed C was chosen according to Schindler and Comita (1972) equal to 11.25 kcal (47.09 kJ). This value is intermediate between those proposed by Morel 1978 (9.32) and Platt 1969 (13.30), and close to the 10.00 given by Dufour (1984) for adjacent Ebrié water.

From the solar available energy and the C fixed by phytoplankton, the overall efficiency of the pond (E), the efficiency by biomass unit (E_B) and the quantum yield (Φ , Bannister 1974; Kirk 1983) were calculated from D3, when chlorophyll a concentrations were above 1 mg m^{-3} (Table 1).

Results

1. Climatic conditions

In the southern part of Côte d'Ivoire, March is the most insolated month of the year (Monteny 1984). During the study, total rainfall was of 41.1 mm coming in 3 stormy events (D6 morning, 8.5 mm; D12 night, 15.6 mm; D13 morning, 17.0 mm). Rainy periods induce sharp decreases of air-temperature, and, when occurring during daytime, low insolation. On the working days, average global radiation was $5700 \text{ Wh m}^{-2} \text{ d}^{-1}$, with little day to day variations, except when precipitations occurred.

2. Hydrochemistry

2.1 Temperature

Water temperature at the sampling level averaged 30.5°C during the study. The pronounced daily fluctuations were related to insolation and water characteristics (shallow water, dark color of sediment before colonization, turbidity of water afterwards), with minimum around 6 am ($\approx 27^\circ\text{C}$) and maximum around 4 pm ($\approx 33^\circ\text{C}$). The daily thermic amplitude decreased as the pond volume increased (D 1: 8.0°C , D 16: 4.5°C).

2.2 pH and inorganic C

Spreading lime induced a sharp increase of pH (D 1, 8 am: 10.1). But that alkalization disappeared rapidly, and 48 h later, pH was around 7.5. This

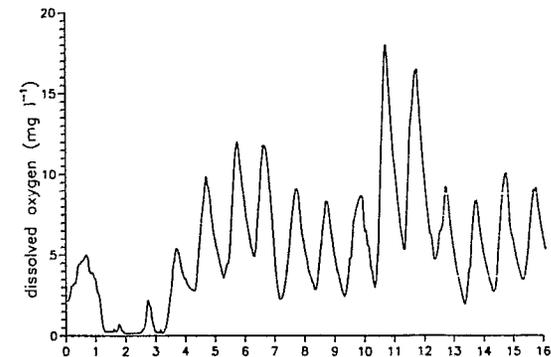


Figure 1. Mean hourly measurement of sub-surface dissolved oxygen. Time units for X-axis: sampling days, D1 (March 15) to D16 (March 31)

parameter variation was then linked to the phytoplanktonic activity (increase of pH from 6 am to 6 pm), but daily pH variation was buffered by water ionization (conductivity: $8000 \mu\text{S cm}^{-1}$). The total alkalinity averaged 2.32 meq l^{-1} during the whole study, with low amplitude day to day variations (around 0.30 meq l^{-1}). Inorganic C concentration averaged 2.41 mg l^{-1} , with clear diel fluctuations. Late afternoon values were between 5 and 20% lower than values observed at dawn.

2.3 Dissolved oxygen

After lime spreading, dissolved oxygen concentrations decreased sharply on D1 evening, and remained close to 0 during the two next days, since biological and/or chemical activities used up all O_2 diffusing through the air-water interface, and there was no new O_2 production. Significant values were observed again from D4 morning. Oxygen concentrations increased at dawn, and decreased when respiration exceeded production (minimum around 7 am, maximum around 4 pm). Daily cycles (Fig. 1) showed important O_2 amplitude variations (D6: 8 mg l^{-1} ; D9: 6 mg l^{-1} ; D11: 12 mg l^{-1}), according to the microalgal biomass development. These differences mainly depended on the daily maximum, since there were no important variations of minimal values (around 3 mg l^{-1}). With these values at ambient high temperatures, pond water was over saturated ($> 150\%$) from mid-morning to 4 pm, and under saturated ($< 50\%$) from evening to the next morning.

3. Suspended particulate matter

3.1 Material $< 63 \mu\text{m}$

3.1.1 Chlorophyll pigments

Pigment concentrations (chlorophyll + phaeopigments) close to 0 at the beginning of the study, increased from D3 (Fig. 2), revealing two successive autotrophic blooms

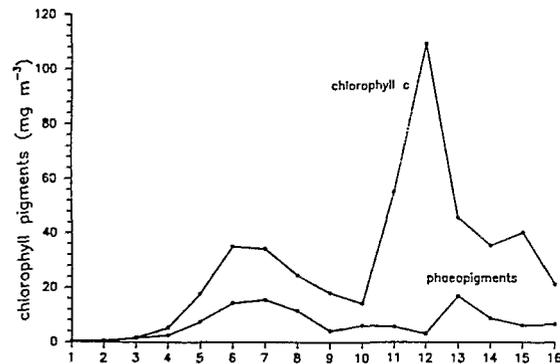


Figure 2. Daily concentrations of chlorophyll a and phaeopigments

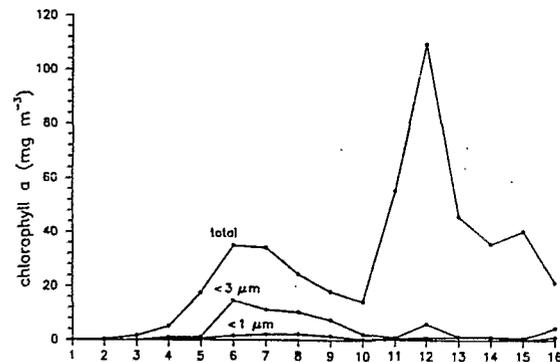


Figure 3. Daily concentrations of chlorophyll a for cells $<1 \mu\text{m}$, $<3 \mu\text{m}$ and total sample

different by their maxima, proportion of degradation pigments and size distribution. The first bloom reached its maximum on D6 (49.2 mg m^{-3}) after an exponential growth from D3. The next one started on D10 and culminated on D12 (112.2 mg m^{-3}). Concentrations then decreased, and on the last day, 27.7 mg m^{-3} were observed. The first bloom showed higher phaeopigment proportions than the second one (around 30% on D6 and D7, but less than 3% on D12). A difference was noted again on chlorophyll a size distribution (Fig. 3): 33% of the first development was based on picoplankton, while the second algal event was largely dominated by nanoplankton, amounting to 95% of the total biomass.

3.1.2 Seston and particulate N

Inorganic and organic seston weights were not very different (respective averages: 10.1 and 12.5 g m^{-3}), but the proportion of organic particles reached 60% of the

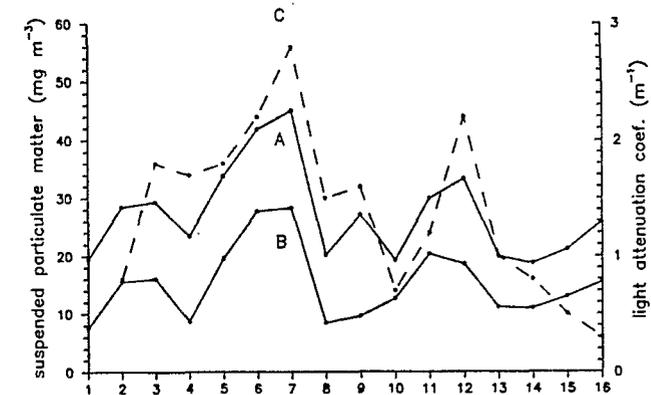


Figure 4. Daily weight of total and organic suspended matter and variation of the mean daily light attenuation coefficient

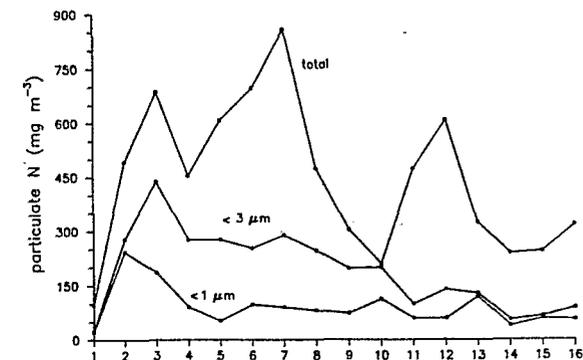


Figure 5. Daily concentrations of N_p for seston $<1 \mu\text{m}$, $<3 \mu\text{m}$ and total sample

total seston during algal blooms (Fig. 4). Mean N_p concentrations were closely related to seston change, with values above 500 mg m^{-3} when phytoplankton was blooming. The low value noted at the beginning of the study (95 mg m^{-3}) reflected the azoic situation of the pond just after lime spreading. As the biological production settled in, higher values were observed, with three development periods. N_p size distributions (Fig. 5) reflected the different colonization steps:

- N_p in seston $<1 \mu\text{m}$ was maximum during precolonization (D2: 243 mg m^{-3} , representing 49% of total N_p). Afterwards, the concentrations decreased without important variations, even if this sort of material amounted for a large part of total N_p between the two algal blooms (D10: 51%).

- for seston with sizes ranging between 1 and 3 μm , N_p values were significantly important only during the first algal development (D3 to D10).
- between D5 and D8, and from D11 to D16, more than 50% of the total N_p was given by seston between 3 and 63 μm .

In order to estimate the percentage of N_p related to phytoplankton, a CHLa/N_p ratio of 3.5 $\mu\text{g CHLa} (\mu\text{mol N})^{-1}$ was used (corresponding to exponentially growing cells. Parsons et al. 1961). According to that value, the respective part of $N_p < 63 \mu\text{m}$ corresponding to active algal cells was estimated. Close to 0 until D3, that part increased progressively, representing 17% of total N_p on D6. A second increase was then noted, with a maximum on D13 (48%). During the first colonization sequence (D2 to D4), the N_p was essentially non-phytoplanktonic, with N_p -equivalent phytoplankton representing at the most 1% of N_p for seston $< 1 \mu\text{m}$, 20% for seston with size ranging between 1 and 3 μm , and 8% of N_p for seston $> 3 \mu\text{m}$. After these first days, N_p in seston $> 1 \mu\text{m}$ was more largely represented by algal cells. On the first bloom, picoplankton represented 13% of N_p -equivalent for seston comprised between 1 and 3 μm ; during the second development, nanoplankton represented 75% of N_p -equivalent for the 3–63 μm size class.

3.2 Seston $> 63 \mu\text{m}$

Before D7, seston $> 63 \mu\text{m}$ represented less than 10% of total seston. After that period of low values, proportions increased rapidly, reaching 27% on D10 and 30% on D14 (7.0 and 8.0 g m^{-3} respectively). Until D7, organic seston $> 63 \mu\text{m}$ represented around 5% of total organic matter. Afterwards, the contribution of these large particles to organic matter increased more rapidly than their contribution to total seston (D10: 28%; D14: 35%). That relative enrichment resulted from an increasing proportion of organic matter in seston $> 63 \mu\text{m}$. A maximum was noted on D14, when total seston amounted to 94% of organic compounds.

For these large particles, high N_p concentrations (220 mg m^{-3}) were observed from D8, with maxima on D9 and D14 (500 and 550 mg m^{-3} respectively). Values were below 30 mg m^{-3} at the end of the study. The relative enrichment of seston by organic matter already described was thus accentuated for N_p , with a part corresponding to seston $> 63 \mu\text{m}$ amounting to 35% on D10, and 56% on D14. That increase in large particle proportion reflected the settling and development of large organisms, with high protein concentrations.

3.3 Light attenuation coefficient (ϵ)

Fluctuations of ϵ closely followed the seston changes (Fig. 4): as particulate matter load decreased with time, water transparency increased progressively. On reduced sestonic load conditions (first days after lime spreading and between two algal blooms), ϵ was $< 1.5 \text{ m}^{-1}$. During the two algal blooms (total seston concentrations largely above 30 g m^{-3}), turbidity was high, and $\epsilon > 2.2 \text{ m}^{-1}$. At the end of study, ϵ was as low as 0.3 m^{-1} .

4. Primary production

4.1 Daily characteristics

When algal photosynthetic activity was effective, around 75% of daily algal production occurred between 8 am and 2 pm. At midday (12–2 pm) insolation was at its maximum, but the activity was equal to or barely higher than during the 2–4 pm sequence. This light saturation phenomenon was also observed on some production depth profiles, mainly during the first algal bloom. Phytoplanktonic C assimilation decreased regularly along with depth, but the theoretical compensation level ($z = 1\%$ of incident energy) above 1.5 m, combined with the low water level in the pond permitted photosynthetic production along the entire water column.

4.2 Temporal evolution

Photosynthetic activity began two days after lime spreading (D2: 53 $\text{mg C m}^{-2} \text{ d}^{-1}$), with chlorophyll a concentration slightly above 1 mg m^{-3} . The variation in primary production followed that of algal biomass, with two peaks on D8 and D12 (1.40 and 2.83 $\text{g C m}^{-2} \text{ d}^{-1}$, Fig. 6). The first event began on D5, reached its maximum 3 days later, ended on D10, and was characterized by a high picoplankton production (D8: 0.32 $\text{g C m}^{-2} \text{ d}^{-1}$, 23% of total primary production). The second event began on D11, reached its maximum the day after and decreased sharply on D13, day characterized by heavy precipitation. Representing less than 1% of total production, picoplanktonic organisms showed a very limited activity during this second bloom. A last event was noted on D14, with a peak on D15 (1.30 $\text{g C m}^{-2} \text{ d}^{-1}$).

4.3 Photosynthetic efficiency

Global efficiency (E , expressed as a percentage) was generally between 0.5 and 1%. Values were particularly low from D3 to D5 (no significant primary production),

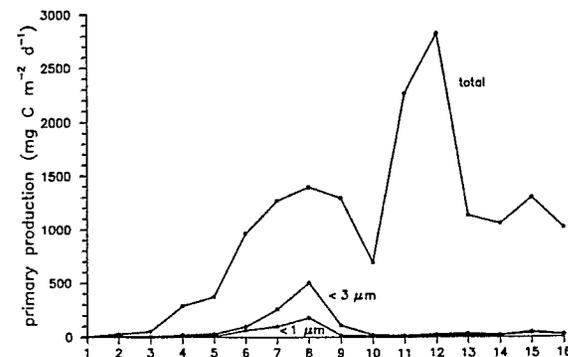


Figure 6. Daily integrated primary production for plankton $< 1 \mu\text{m}$, $< 3 \mu\text{m}$ and total sample

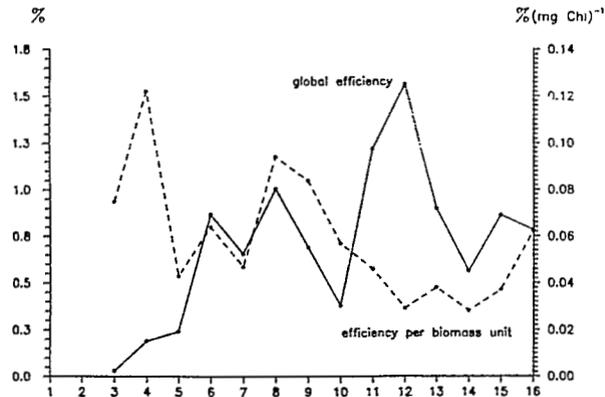


Figure 7. Daily variation of phytoplankton global efficiency and efficiency per biomass unit

and the highest efficiency was noted on D 12 (1.6%), at the maximum of the second algal bloom (Fig. 7). For the whole phytoplanktonic community, efficiency per biomass unit (E_B) was often $> 0.05\%$ (mg chl^{-1}) during the first bloom, while the second event was rather characterized by lower values (0.02 to 0.05% (mg chl^{-1})). At the end of the study, efficiency per biomass unit increased significantly reaching values close to those observed during the first bloom, while chlorophyll concentrations were decreasing. E_B for picoplankton was higher than 0.05% (mg chl^{-1}) before and during the first algal bloom (D 3, D 5 and D 8: 0.14, 0.06 and 0.06% (mg chl^{-1})). For these small cells, efficiency was usually lower than 0.02% (mg chl^{-1}). Nanoplankton efficiency per biomass unit was always higher, ranging between 0.03 and 0.14% (mg chl^{-1}). The quantum efficiency for total phytoplankton (Φ) was higher during the first algal development (0.057 mole C mole⁻¹) than during the second one (0.019 mole C mole⁻¹). For the whole study, the mean Φ corresponding to nanoplankton was also higher (0.042 mole C mole⁻¹) than the mean Φ calculated for picoplankton (0.020 mole C mole⁻¹).

4.4 Nitrogen supply and demand

The amount of Nitrogen fixed by phytoplankton (its "demand") was estimated from the Redfield's atomic ratio through the primary production values. To that demand corresponded a "supply" from the system, which was the N available for cells, here essentially N-NH₄ furnished by ground water. The demand/supply ratio was very low at the beginning of the study. The first algal bloom induced an increase of that parameter, demand representing more than 20% of supply on D 8. An increase of the ratio was also observed at the beginning of the second bloom (D 11: 42%; D 12: 69%), after what the demand decreased toward 30%. An extrapolation of the increasing trend between D 10 and D 12 showed that algal demand might have exceeded supply on D 14.

Discussion

1. Succession during colonization

The immediate effects of lime spreading are to induce water clarification (siston precipitation) and to sterilize relatively the sediment and the water remaining in the pond (increase of temperature and pH). Indirectly, CaCO₃ addition induces water alkalization (alkalinity is 6 times higher in the pond, compared to water of Ebríe lagoon at the same conductivity), and C availability under CO₂ form (Arce and Boyd 1975; Hunt and Boyd 1981). It also accelerates the fractionation of organic materials, and thus, favors further mineralization. Alkaline products input allows also the decomplexation and the diffusion in the entire water column of humic compounds precedently adsorbed on organic-clay complex (Kononova 1961). However, since the pond banks are not treated, residual water holes such as fish galleries will constitute shelters for organisms which will in turn recolonize the pond as these isolated holes are progressively flooded by ground water. Species presenting the highest growth potential will preferentially develop in such enriched water.

Alkaline conditions (pH around 10) and abundance of energetic labile substrates will first favour the development of microorganisms, showing very short doubling time. Their proliferation rapidly induces a doubling of ϵ , an exhaustion of dissolved oxygen and a sharp increase of N_p, which contains more than 50% of particles $< 3 \mu\text{m}$. Then, an alkalinity decrease will make possible the development of photosynthetic organisms enduring very high organic loads and accepting N-NH₄ as major inorganic N supply. That bloom is based on small cells (essentially Cyanobacteria: *Romeria gracilis*, *Lyngbya limnetica*) with particular nutrition (ability to use organic and ammonia N, Neilson and Larson 1980) and growth characteristics, close to those of bacteria. This pioneer photosynthetic activity induces a positive O₂ balance regarding to heterotrophic respiration. Six days after lime spreading, 42% of total pigment concentration (35.0 mg Chl a m⁻³) are represented by picoplankton. That development is exponential from D 3, and is maximum on D 6, with doubling times for pico and nanoplankton: 9.6 and 19.2 h respectively. Competition with bacteria for N substrates induces a 78% decrease of non-photosynthetic N_p for particles $< 1 \mu\text{m}$. The higher ϵ (2.8 m⁻¹), maximum organic seston weights (28.3 g m⁻³) and N_p $< 63 \mu\text{m}$ concentrations (0.86 g m⁻³) observed during the study correspond to that step. Total N_p was largely represented by particles comprised between 1 and 3 μm , but only 15% of the N_p of that size class was represented by photosynthetic organisms. Moreover, 31% of total pigments are made up of phaeopigments.

Thus, microzooplanktonic grazers (ciliates, flagellates) are associated to that first bloom with high picoplankton participation, exploiting and controlling the microalgal biomass (Arfi and Guiral, submitted). That predation results in a decrease of organic seston, N_p and pigments (parameters reflecting biomass), a corresponding decrease of water turbidity, and a halt in the increase of daily amplitude of dissolved O₂.

This grazing of picoplankton is favourable to nanoplankton proliferation (essentially Chlorophyta: *Coelastrum microsporum*, *Coenocystis reniformis*), growing exponentially from D 10 to D 12. Seston $< 63 \mu\text{m}$ will then be represented essentially

by large cells, fixing an increasing part of N_p (up to 66% of $N_p < 63 \mu\text{m}$). Chlorophyll a values are 2.3 times higher in concentration, and 3 times higher in load during the second bloom than during the first one. The contribution of picoplankton to that second bloom is minor (1.6% of the total biomass, with a doubling time of 26.4 h). The rapid development of large cells limits the picoplankton access to trophic and energetic resources, in addition to the selective grazing pressure. The high activity of nanoplankton (doubling time: 12 h) is here accompanied by zooplanktonic developments (organisms with high protein concentrations: 41% of total N_p), essentially based on Rotifers (*Brachionus plicatilis* and *Hexarthra intermedia*, Legendre et al. 1987; Arfi and Guiral submitted). The sharp decrease of pigment biomass since D13 is also reflected by a marked reduction of organic seston, water turbidity and daily O_2 variations. This fast decrease in chlorophyll a concentration is not accompanied by an increase of phaeopigment values: therefore, grazing is not the only mechanism in this process.

2. Primary production controls

The primary production values observed in this pond without fertilization are significant (maximum: $2.8 \text{ g C m}^{-2} \text{ d}^{-1}$), and comparable to those reported for other tropical areas in fertilized ponds: Israel (Hepher 1962: 3.3 to $6.4 \text{ g C m}^{-2} \text{ d}^{-1}$; Zur 1981: 2.3 to $8.1 \text{ g C m}^{-2} \text{ d}^{-1}$; Motzkin et al. 1982: $2.0 \text{ g C m}^{-2} \text{ d}^{-1}$), Alabama (Almagan and Boyd 1978: 1.0 to $3.1 \text{ g C m}^{-2} \text{ d}^{-1}$), Malaysia (Moriarty et al. 1983: 0.8 to $1.6 \text{ g C m}^{-2} \text{ d}^{-1}$). Yet, the values are far greater than those observed in Ebrié lagoon near Layo ($0.3 \text{ g C m}^{-2} \text{ d}^{-1}$, Pagès et al. 1981). Alimanted by ground and lagoon waters, these ponds are naturally enriched systems, with high primary production potentialities. This biological activity is rapidly observed after lime spreading, when pH values decrease to less than 8. Picoplankton plays a large role in the pioneer community, reaching a maximum of $15.1 \text{ mg Chla m}^{-3}$ (or $5.9 \text{ mg Chla m}^{-2}$, 42% of active biomass), and contributing up to 36% to primary production ($0.50 \text{ g C m}^{-2} \text{ d}^{-1}$). These values confirm picoplankton importance in aquatic ecosystems (Stockner and Antia 1986). They are superior to those reported for picoplankton in oceanic or continental ecosystems (Table 2).

Growth rates for pico and nanoplankton were calculated the following way: microalgal biomass expressed in C for p- and nanoplankton was calculated from morning chlorophyll data using experimentally determined Carbon/chlorophyll ratio (respectively: 30 and 40 mg/mg, Arfi, unpublished). To that pool (C_0) was added the inorganic C assimilation deduced from the daily ^{14}C incorporation per size class, giving the pico and nanoplankton carbon at the end of the photoperiod (C_1). Assuming exponential increase in biomass, growth rates were defined as $(\ln C_1 - \ln C_0)/12$. Average C-assimilation rates are 0.09 h^{-1} for picoplankton and 0.12 h^{-1} for nanoplankton, with, in both cases, coefficients of variation close to 25%. A non-parametric average comparison test (Mann and Whitney) shows a 5% significant difference. At the most, the C-assimilation rate for picoplankton and nanoplankton are then equal. For these organisms with a high growth rate, that

Table 2. Picoplankton biomass and production from reference data

Location	Production $\text{mg C m}^{-3} \text{ h}^{-1}$	Biomass mg Chla m^{-3}	References
Freshwater, oligotrophic			
Great Central lake (Canada)	0.7	1.0	Costello et al. (1979)
Lake Superior (USA)	0.6	0.3	Munawar and Fahnenstiel (1982)
Freshwater, eutrophic			
Layo (Côte d'Ivoire)	41.7	14.7	This work
Marine ecosystems			
Tropical Pacific	4.1	1.0	Li et al. (1983)
Sub-tropical Pacific	1.5	0.1	Bienfang and Takahashi (1983)
Pacific (Hawaii)	7.6	0.2	Bienfang and Szyper (1981)
Pacific (California)	2.2	1.4	Putt and Prezelin (1985)
Tropical Atlantic	0.5	1.1	Platt et al. (1983)

paradoxical result may be explained by their sensibility to the received energy. The daily light-integrated value includes sequences of very high insolation, inducing temporary photo-inhibition phenomena, particularly during the first days, when water level is minimum in the pond.

The global efficiency of primary producers in the pond was scarcely higher than 1% (maximum on D12: 1.6%). But the fluctuations of that parameter are closely linked to primary production, and the two blooms succession is well described, the second one showing the highest efficiency. These values are lower than those observed in eutrophic Ethiopian lakes (3.3%, Talling et al. 1973) or lake Kinneret (4%, Dubinsky and Berman 1981). Expressed by biomass unit, the efficiency differed along with the different colonization steps.

Nanoplankton quantum efficiency is also higher than the Φ calculated for smaller algae, even when picoplankton represents a large part of the total algal biomass. Values for Φ are high during the first bloom, when ϵ is still high ($> 1.8 \text{ m}^{-1}$). For less turbid waters, only a reduced part of the available energy can be used by the cells, unused radiation being dissipated as heat or fluorescence (Kirk 1983; Dubinsky et al. 1984). Highest values are noted during high turbidity periods, when bacteria (D3: $\epsilon = 1.8 \text{ m}^{-1}$), then phytoplankton (D7: $\epsilon = 2.8 \text{ m}^{-1}$) developments are important. The proliferation of nanoplankton during the second bloom has not the same self-shading effect and the quantum efficiency decreased sharply during the second bloom. This may be explained by the fact the larger cells diffuse less light than the small ones.

Since the primary production is not directly controlled through inorganic C availability (average concentrations $> 2.4 \text{ mmol l}^{-1}$), its fluctuation will closely follow that of chlorophyll biomass. During the two blooms, the sharp activity decrease, closely following exponential development, implies the existence of other regulatory mechanisms. The first bloom was mainly controlled by micrograzers (Arfi

and Guiral submitted). This is in agreement with the decrease of photosynthetic organisms in the $<3 \mu\text{m}$ size class, and the increase in phaeopigments in this class. For the second event, comparison of N demand and supply shows that efficiency decreased when the demand for N exceeded 40% of supply. Decrease in biomass was noted from D 13, on which the demand represented 69% of supply. On D 14, this sharp regulation induced a 50% biomass reduction, and N demand fell to less than 30% of N supply. Temporary N limitation and grazing by rotifer (Arfi and Guiral submitted) have probably combined their effects for primary production control, along with particular climatic conditions, inducing the sharp decline of the second bloom and slowing the evolution toward a more diversified zooplanktonic community (Legendre et al. 1987).

Conclusion

From March 15 to March 31 1988, the system development in the Layo pond (trophic state, biological structure) went through 3 stages during its early recolonization:

- until March 18, precolonization by an heterotrophic bacterial community, which exploited the high organic load present in the pond after partial drying and lime spreading;
- pioneer colonization by a microalgal community, where picoplankton was largely represented. An active consumption of that biomass by microzooplankton induces its rapid decrease, and selection of larger planktonic algae;
- from March 25, the second microalgal colonization (essentially nanoplankton). Its considerable development induces a temporary exhaustion of inorganic N; that phenomenon, in addition to the active grazing by a zooplanktonic community largely dominated by rotifers brings about the microalgal biomass adjustment to the system's actual trophic potentialities.

Phases of photosynthetic productivity with various intensities correspond to these chlorophyll biomass variations, and the intensities culminate at the times of either microalgal bloom. The first peak ($1.40 \text{ g C m}^{-2} \text{ d}^{-1}$) is observed 8 days after lime spreading, and is followed 5 days later by a second development ($2.83 \text{ g C m}^{-2} \text{ d}^{-1}$). The differences between these two production peaks are of the same order as those between biomass maxima. For sequences with significant phytoplankton biomass (beginning 4 days after spreading), primary production fluctuated between 0.50 and $2.83 \text{ g C m}^{-2} \text{ d}^{-1}$, which can be compared to the value of $0.30 \text{ g C m}^{-2} \text{ d}^{-1}$ reported in the near-by lagoon waters. This photosynthetic activity is directly controlled by the algal biomass and the differential efficiency of the algal communities, as structured by grazing. At the end of the precolonization period, the nutrient availability is an additional regulation process.

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